Distribution of the Bonnet Limpet, *Hipponix conicus* (Gastropoda: Hipponicidae), among Host Species in Western Kyushu, Japan

KAZUNORI YAMAHIRA[1] AND FUMITO YANO

Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Reihoku-cho, Amakusa, Kumamoto 863-25, Japan

Abstract. The bonnet limpet, *Hipponix conicus* (Schumacher, 1817), adheres to the shell surface of other snail species. In order to discuss the ecological relationships between *H. conicus* and many host snails, the distribution of this limpet among its potential hosts was determined in western Kyushu, Japan. A total of 26 snail species was collected, and *H. conicus* was found on 13 of them. The mean adhesion frequencies and mean numbers of *H. conicus* per snail were significantly different among the host species. Among eight host species, more *H. conicus* were found on shells with living snails than on shells with hermit crabs. The number of *H. conicus* per host and shell length of *H. conicus* tended to increase with host size for 11 and eight host species, respectively. Host snail individuals with at least one *H. conicus* tended to be larger than those without any *H. conicus* for ten species. Overall, our data indicate that the quality of shells as a host differs among host species (living snails and hermit crabs) or host sizes. The difference in *H. conicus* loads could be caused primarily by preferential adhesion to different hosts and/or differential growth and/or survival on different hosts.

INTRODUCTION

The bonnet limpet, *Hipponix conicus* (Schumacher, 1817), attaches to shells of many different species of marine gastropods in Japan, including commercially important ones, such as the Japanese abalone, *Haliotis aquatilis* (Reeve, 1846) and the turban shell, *Turbo cornutus* (Lightfoot, 1786) (Matsunaga, 1964). However, bivalves never harbor *H. conicus* (Matsunaga, 1964). *Hipponix conicus* reproduces on host snails by direct development (i.e., there is no pelagic stage) (Habe, 1953; Amio, 1963); and several authors (Yonge, 1953, 1960; Cernohorsky, 1968; Knudsen, 1991) postulated that it is a protandrous, consecutive hermaphrodite.

Hipponix conicus is often observed to deeply erode the shell of its host species (Knudsen, 1991) and therefore has been suggested to reduce their market value (Matsunaga, 1964). In particular, it appears that *H. conicus* adheres more strongly to cultured varieties of host species than to natural forms, probably resulting in severe economic damage. To date, however, little attention has been paid to interactions between *H. conicus* and host species. Matsunaga (1964) investigated the ecological relationship between *H. conicus* and *Haliotis aquatilis* with respect to the adhesional position on the host and movement between host individuals. He stated that *H. conicus* tended

to adhere near respiratory pores to eat feces or soft parts of the host, and that *H. conicus* sometimes moved among host individuals in pursuit of better habitats. On the other hand, Knudsen (1991) argued that it is unlikely that fecal pellets of the host would constitute an essential part of the food of *Hipponix australis* (Lamarck, 1819), similar to and taxonomically confused with *H. conicus,* and that *H. australis* is not selective as to its choice of gastropod host, because a wide variety is used. However, the earlier authors did not conduct a quantitative survey of the preference of *Hipponix* species for host gastropod species, which would be primary information regarding the ecological relationship among them.

This paper describes the distribution of *H. conicus* among many potential host species inhabiting intertidal to shallow subtidal zones, and examines some ecological relationships between *H. conicus* and the host species. In particular, the differential *H. conicus* loads among different species and different sizes of hosts are discussed from the viewpoint of preferential adhesion to different hosts (host preference), differential growth and/or survival on different hosts (host quality), and differences in exposure to *H. conicus* among hosts (opportunity for adhesion).

MATERIALS AND METHODS

Our study was carried out during the spring low tides of October 1994 at Magarisaki spit, Amakusa Shimo-shima Island, western Kyushu, Japan (32°32′N, 130°2′E). Fifty-six 50 × 50 cm quadrats were set in the low intertidal

Present address: Department of Environmental Chemistry, Faculty of Engineering, Kyushu Kyoritsu University, Kitakyushu 807-8585, Japan; e-mail: yamahira@kyuko-u.ac.jp

(0.4 m above mean low water spring tide: MLWS) and subtidal zone (0.6–2.6 m below MLWS). One or two layers of boulders (mean diameter approx. 20–30 cm) covered the substrate in all quadrats. On the beach, grazer snails and chitons are abundant (Takada & Kikuchi, 1990). All living snails and shells with hermit crabs in each quadrat were collected, transported to the laboratory, and fixed in 10% neutralized formalin. SCUBA diving was used for collecting in the subtidal zone. In the laboratory, all snails and shells were identified, and their size was measured with vernier calipers (±0.05 mm). Either shell length or shell width was used as a size indicator of each of the snail species. Because shell length represents their sizes better than shell width for some species and vice versa for the others, we used appropriate measurements for each species. All shells were examined for the presence of *Hipponix conicus*. Adhesion frequencies of each host species (proportion of individuals with at least one *H. conicus*) were calculated for each quadrat, and the number of *H. conicus* on each shell was counted; then the shell length (length between the anterior and posterior edge) of each *H. conicus* was measured with the vernier calipers. Almost all of the *H. conicus* individuals remained on the shells through the fixation and handling (only a few were observed off from their hosts). Thus, the observed distribution patterns of *H. conicus* among hosts were considered to be natural, not artifactual.

Kruskal-Wallis tests were used to determine if there were significant differences among host species in the adhesion frequencies in each quadrat and in the number of individuals per host. To compare *H. conicus* adhesion frequencies and numbers on shells with living snails and those with hermit crabs, Mann-Whitney U tests were used for each of the nine snail species whose shells were utilized by both *H. conicus* and hermit crabs. For each of the 12 snails species that harbor *H. conicus,* we determined if the number and size of *H. conicus* was significantly correlated with the size of its host. Furthermore, to determine if larger hosts were more likely to harbor *H. conicus,* we compared the shell sizes of snails with and without *H. conicus* for each host species using Mann-Whitney U tests.

RESULTS

A total 26 snail species were collected from the site (Table 1); six species (23%) were found only in the low intertidal zone, 13 species (50%) were only in the subtidal zone, and seven species (27%) were found in both. Thirteen species (50%) had at least one *Hipponix conicus* attached. *Hipponix conicus* was found on snail species collected from both tidal zones. However, only two *Tectus pyramis* individuals were collected, and they are excluded in all analyses below. No *H. conicus* was found living attached on the surface of boulders.

Mean adhesion frequencies ranged from 0.04 (*Japeu-*

thria ferrea) to 1.0 (*Thais bronni*) (Table 2), and they were significantly different among host species (Kruskal-Wallis test, *P* < 0.0001). Mean numbers of *H. conicus* per host individual ranged from 0.08 (*J. ferrea*) to 6.17 (*T. bronni*) (Table 3) and were significantly different among host species (Kruskal-Wallis test, *P* < 0.0001). In host species that have higher adhesion frequencies, individual snails tended to carry more *H. conicus:* there was a significant positive correlation between the mean adhesion frequencies for a species and mean number of *H. conicus* per individual (*r* = 0.86, *P* = 0.0003, n = 12).

The mean adhesion frequencies were higher on living snails than on hermit crab shells for all nine species (Table 2). The adhesion frequencies were significantly different for five of the nine species, though the sample size of hermit crabs was rather small. The mean numbers of *H. conicus* per shell were also higher on living snails than on hermit crab shells for eight of the nine species (Table 3), and the differences were significant in five of the eight species.

In general, the number of *H. conicus* per host increased with host size (Table 4). In five of the 12 species, there was significant positive correlation between the number of *H. conicus* per host and host size. *H. conicus* shell length also increased with host size in eight of the 11 host species (Table 5), but the correlation was significant in only two of the eight species. Furthermore, snail individuals with at least one *H. conicus* were larger than snails without any *H. conicus* in ten of the 11 host species (Table 6), and in three of the ten species, the difference was significant.

DISCUSSION

Although we observed that *Hipponix conicus* loads differed among host species, these differences could be caused by preferential adhesion to different host species (host preference), differential growth and/or survival on different host species (host quality), or differences in exposure to *H. conicus* among host species. Comparison between the snail species frequently adhered to and those infrequently or never adhered to appears to say little about the conditions under which *H. conicus* adheres. No predictions about a species' *H. conicus* load can be made based on taxonomic group, morphological features, or foraging habits. However, it seems that *H. conicus* is infrequently found on species with the following characteristics: (1) small size (e.g., *Mitrella bicincta, Trochus sacellus*); (2) ability to cover themselves with a mantle (e.g., *Purpuradusta gracilis, Adusta onyx*); (3) covered by calcareous algae (e.g., *Astralium haemafragum*); and (4) ability to move to the higher intertidal zone (*Monodonta labio, Japeuthria ferrea*; see Takada, 1996; N. Ota, unpublished data). These characteristics might decrease the shell's quality as a host or the exposure time to *H. conicus.*

Table 1

Mean shell size (±SD) of living snails collected at the study site. Either shell length (SL) or shell width (SW) was measured as a size indicator of each of the snail species. Y (Yes) and N (No) indicate whether the species has at least one *Hipponix conicus* attached or not, respectively.

Snail species	Measured part	Mean ± SD mm (n)	Presence of *Hipponix conicus*
Found only in the intertidal zone			
Clanculus ater (Pilsbry, 1901)	SW	7.18 ± 5.20 (2)	N
Monodonta labio (Tapparone-Canefri, 1874)	SW	13.64 ± 1.89 (31)	N
Chlorostoma argyrostoma (Tapparone-Canefri, 1874)	SW	21.23 ± 2.91 (67)	Y
Lunella coronata (Récluz, 1853)	SW	19.70 ± 1.28 (132)	Y
Japeuthria ferrea (Reeve, 1847)	SL	22.66 ± 4.80 (12)	Y
Thais clavigera (Küster, 1858)	SL	24.40 (1)	N
Found in both the intertidal and subtidal zone			
Cantharidus japonicus (Adams, 1853)	SL	6.77 ± 1.59 (3)	N
Omphalius nigerrima (Gmelin, 17919)	SW	18.33 ± 1.25 (10)	Y
Omphalius rusticus (Philippi, 1846)	SW	17.55 ± 4.42 (181)	Y
Turbo stenogyrun (Fischer, 1873)	SW	16.26 ± 5.24 (7)	Y
Ergalatax contractus (Reeve, 1846)	SL	17.75 ± 3.92 (367)	Y
Mitrella bicincta (Gould, 1860)	SL	9.44 ± 1.11 (26)	N
Pyrene scripta (Lamarck, 1822)	SL	14.28 ± 1.66 (182)	Y
Found only in the subtidal zone			
Calliostoma unicum (Dunker, 1860)	SW	16.93 ± 2.98 (3)	N
Omphalius pfeifferi (Philippi, 1846)	SW	21.15 ± 3.19 (40)	Y
Trochus sacellus (Dunker, 1862)	SW	16.10 (1)	N
Tectus pyramis (Born, 1778)	SW	26.80 ± 6.15 (2)	Y
Astralium haemafragum (Menke, 1829)	SW	18.49 ± 3.92 (49)	Y
Conomurex luchuanus (Linnaeus, 1758)	SL	58.15 (1)	N
Adusta onyx (Linnaeus, 1758)	SL	39.85 (1)	N
Purpuradusta gracilis (Schilder, 1931)	SL	15.95 ± 1.78 (6)	N
Thais echinata (Blainville, 1832)	SL	40.25 (1)	N
Thais bronni (Dunker, 1860)	SL	27.43 ± 10.11 (6)	Y
Thais luteostoma (Holten, 1803)	SL	24.33 ± 6.11 (42)	Y
Mitra scutulata (Gmelin, 1791)	SL	28.65 (1)	N
Pusia inermis (Reeve, 1845)	SL	10.70 (1)	N

Table 2

Mean adhesion frequency (±SD) of each host shell with living snails and hermit crabs. Mann-Whitney U test: * and ** denote the significant difference at 5% and 1% level, respectively.

Host species	Mean ± SD (n)		P
	Living snail	Hermit crab	
Thais bronni	1.00 ± 0.00 (5)	—	
Omphalius nigerrima	0.96 ± 0.09 (5)	0.00 ± 0.00 (2)	0.0134*
Thais luteostoma	0.95 ± 0.14 (23)	0.00 ± 0.00 (2)	0.001**
Omphalius pfeifferi	0.94 ± 0.14 (19)	0.75 ± 0.50 (4)	0.5394
Omphalius rusticus	0.63 ± 0.32 (25)	0.11 ± 0.33 (9)	0.0004**
Chlorostoma argyrostoma	0.38 ± 0.32 (13)	0.10 ± 0.32 (10)	0.018*
Lunella coronata	0.38 ± 0.17 (16)	0.25 ± 0.50 (4)	0.1293
Ergalatax contractus	0.32 ± 0.29 (51)	0.06 ± 0.25 (16)	0.0003**
Astralium haemafragum	0.27 ± 0.38 (25)	—	
Turbo stenogyrun	0.13 ± 0.25 (4)	0.00 (1)	0.6171
Pyrene scripta	0.09 ± 0.18 (46)	0.00 ± 0.00 (3)	0.2501
Japeuthria ferrea	0.04 ± 0.12 (8)	—	

Table 3

Mean number (±SD) of *Hipponix conicus* per host shell with living snails and hermit crabs. Mann-Whitney U Test: * and ** denote the significant difference at 5% and 1% level, respectively.

Host species	Mean ± SD (n)		P
	Living snail	Hermit crab	
Thais bronni	6.17 ± 4.58 (6)	—	
Thais luteostoma	5.88 ± 5.64 (42)	0.00 ± 0.00 (2)	0.0271*
Omphalius pfeifferi	4.35 ± 3.89 (40)	5.50 ± 6.14 (4)	1.0000
Omphalius nigerrima	1.90 ± 1.20 (10)	0.00 ± 0.00 (2)	0.0478*
Turbo stenogyrum	1.57 ± 3.05 (7)	0.00 (1)	0.5677
Omphalius rusticus	1.43 ± 2.02 (181)	0.04 ± 0.20 (24)	0.0001**
Ergalatax contractus	0.84 ± 1.34 (367)	0.18 ± 0.85 (22)	0.0013**
Chlorostoma argyrostoma	0.78 ± 1.00 (67)	0.05 ± 0.23 (19)	0.0012**
Lunella coronata	0.61 ± 0.98 (132)	0.33 ± 0.82 (6)	0.4037
Astralium haemafragum	0.39 ± 1.04 (49)	—	
Pyrene scripta	0.13 ± 0.48 (182)	0.00 ± 0.00 (3)	0.5677
Japeuthria ferrea	0.08 ± 0.29 (12)	—	

Hipponix conicus was more likely to be found on living snails than on shells inhabited by hermit crabs. This fact suggests that living snails might promote growth and/or survival of *H. conicus*. Matsunaga (1964) reported that *H. conicus* uses its prolonged proboscis to eat the feces and mantle of the host snail. Laws (1971) concluded that *H. conicus* is a particle feeder that benefits from the particles carried with the afferent current produced by hosts. On the other hand, Knudsen (1991) argued that fecal pellets of hosts do not constitute an essential part of the food of *Hipponix*.

Larger hosts possessed more, larger *H. conicus,* probably due to preferential adhesion to larger hosts (host preference), differential growth, and/or survival on different-sized hosts (host quality). Large hosts may provide more surface area for adhesion and more food. Spatial and food resources are expected to be more limited on small hosts, causing intraspecific competition between *H. conicus* individuals on the same host. Density-dependence in growth or survival has been reported in many other organisms (e.g., Begon et al., 1990). Also, the larger hosts may experience less predation pressure, providing a more stable environment. Overall, larger hosts may have higher quality.

In contrast, larger *H. conicus* loads on larger hosts might be due to differences in exposure time to *H. conicus* among size-classes of hosts, that is, since larger hosts may be merely older than smaller ones, they might have been adhered to by more and larger (well grown) *H. conicus*. To reject this hypothesis, we have to examine

Table 4

Correlation coefficients (*r*) between host size and number of *Hipponix conicus* per host. Fisher F to z test: * and ** indicate that the correlation was statistically significant at 5% and 1% level, respectively.

Host species	r (n)	P
Thais bronni	0.080 (6)	0.8893
Thais luteostoma	0.543 (42)	0.0001**
Omphalius pfeifferi	0.476 (40)	0.0017**
Omphalius nigerrima	−0.374 (10)	0.2990
Omphalius rusticus	0.509 (181)	<0.0001**
Chlorostoma argyrostoma	0.233 (67)	0.0571
Lunella coronata	0.183 (132)	0.0359*
Astralium haemafragum	0.131 (49)	0.3710
Ergalatax contractus	0.258 (367)	<0.0001**
Turbo stenogyrum	0.674 (7)	0.1021
Pyrene scripta	0.127 (182)	0.0877
Japeuthria ferrea	0.501 (12)	0.0982

Table 5

Correlation coefficients (*r*) between host size and size of *Hipponix conicus*. Fisher F to z test: * and ** indicate that the correlation was statistically significant at 5% and 1% level, respectively.

Host species	r (n)	P
Thais bronni	0.278 (40)	0.0819
Thais luteostoma	0.041 (247)	0.5180
Omphalius pfeifferi	0.234 (175)	0.0017**
Omphalius nigerrima	0.160 (19)	0.5191
Omphalius rusticus	−0.024 (255)	0.7042
Chlorostoma argyrostoma	0.177 (52)	0.2109
Lunella coronata	0.226 (80)	0.0434*
Astralium haemafragum	−0.254 (18)	0.3143
Ergalatax contractus	0.086 (309)	0.1333
Turbo stenogyrum	−0.209 (11)	0.5493
Pyrene scripta	0.070 (23)	0.7534
Japeuthria ferrea	—	—

Table 6

Mean size (±SD) of snail individuals with at least one *Hipponix conicus* attached and those without any *Hipponix conicus*. Mann-Whitney U test: ** denotes the significant difference at 1% level.

Host species	Mean ± SD mm (n)		P
	Attached	Not attached	
Thais bronni	27.43 ± 10.11 (6)	—	
Thais luteostoma	24.33 ± 6.05 (39)	24.38 ± 8.35 (3)	0.9028
Omphalius pfeifferi	21.44 ± 2.96 (36)	18.60 ± 4.59 (4)	0.241
Omphalius nigerrima	18.44 ± 1.27 (9)	17.30 (1)	0.3826
Omphalius rusticus	20.29 ± 1.85 (89)	14.89 ± 4.57 (92)	0.0001**
Chlorostoma argyrostoma	21.93 ± 2.37 (31)	20.62 ± 3.22 (36)	0.1102
Lunella coronata	19.99 ± 1.03 (48)	19.54 ± 1.39 (84)	0.0692
Astralium haemafragum	20.24 ± 2.33 (11)	17.98 ± 4.15 (38)	0.2083
Ergalatax contractus	19.16 ± 2.71 (153)	16.74 ± 4.32 (214)	0.0001**
Turbo stenogyrum	28.23 ± 4.28 (2)	16.25 ± 2.10 (5)	0.0528
Pyrene scripta	15.06 ± 0.72 (18)	14.19 ± 1.71 (164)	0.005**
Japeuthria ferrea	30.30 (1)	21.96 ± 4.36 (11)	0.1924

whether larger hosts are preferred by larger *H. conicus* disproportionately to their ages. Assuming that the size of each host snail is proportional to its age, it was found that in some host species larger individuals suffered adhesion by a significantly larger number of larger *H. conicus* than predicted (Yamahira, unpublished data), suggesting that differences in exposure time would not be the cause of the differential loads among size-classes of hosts.

Matsunaga (1964) stated that *H. conicus* sometimes moves among host individuals in pursuit of better habitats. The extremely biased loads of *H. conicus* among the species or size-classes of hosts in our study suggests that they actively migrate among host individuals. Although no *H. conicus* was found living attached on the surface of boulders in the present study, there are also reports of *Hipponix* being independent of gastropod shells and settling on rocks (Matsunaga, 1964, for *H. conicus*; Macpherson & Gabriel, 1962, for *H. australis*). But, the migration might occur very infrequently because some authors have argued that *Hipponix* is unable to move after settling (Knudsen, 1991; and references therein). In addition, *Hipponix* might be able to migrate only in the earlier stage of their life cycle because they adapt their shell margin to the configuration of substratum as they grow (Knudsen, 1991). In the slipper limpet, *Crepidula adunca*, living on the shells of other gastropods and reproducing by direct development like *Hipponix*, dispersal of newly hatched juveniles has been observed (Putnam, 1964).

In conclusion, this study has demonstrated that the distribution of *H. conicus* was remarkably different among host species or host sizes. These findings suggest that the quality of the snails as a host differs among host species or host sizes. The difference in *H. conicus* loads could be caused primarily by preferential adhesion to different hosts and/or differential performances on different hosts.

LITERATURE CITED

AMIO, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. Journal of Shimonoseki University of Fisheries 12:15–144. [in Japanese with English summary].

BEGON, M., J. L. HARPER & C. R. TOWNSEND. 1990. Ecology: Individuals, Populations, and Communities. 2nd ed. Blackwell: Oxford.

CERNOHORSKY, W. O. 1968. Observations on *Hipponix conicus* (Schumacher, 1817). The Veliger 10:275–280.

HABE, T. 1953. Studies on the eggs and larvae of the Japanese gastropods. Publications of the Seto Marine Biological Laboratory 3:161–167.

KNUDSEN, J. 1991. Observations on *Hipponix australis* (Lamarck, 1819) (Mollusca, Gastropoda, Prosobranchia) from the Albany area, Western Australia. Pp. 641–660 in F. E. Wells, D. I. Walker, H. Kirkman & R. LETHBRIDGE (eds.), Proceedings of the Third International Marine Biological Workshop. The Marine Flora and Fauna of Albany, Western Australia. Vol. II. Western Australian Museum: Perth.

LAWS, H. M. 1971. Reproductive biology and shell site preference in *Hipponix conicus* (Schumacher). The Veliger 13: 115–121.

MACPHERSON, J. H. & C. J. GABRIEL. 1962. Marine Molluscs of Victoria. Melbourne University Press: Melbourne.

MATSUNAGA, N. 1964. Remarks on the ecological observation of a Japanese hoof shell, *Hipponix (Sabia) conicus* (Schumacher). Venus (Japanese Journal of Malacology) 23:149–157 [in Japanese with English summary].

PUTNAM, D. A. 1964. The dispersal of young of the commensal gastropod *Crepidula adunca* from its host, *Tegula funebralis*. The Veliger 6(Suppl.):63–66.

TAKADA, Y. 1996. Vertical migration during the life history of the intertidal gastropod *Monodonta labio* on a boulder shore. Marine Ecology Progress Series 130:117–123.

TAKADA, Y. & T. KIKUCHI. 1990. Mobile molluscan communities in boulder shores and the comparison with other intertidal habitats in Amakusa. Publications from the Amakusa Marine Biological Laboratory, Kyushu University 10:145–168.

YONGE, C. M. 1953. Observations on *Hipponix antiquatus* (Linnaeus). Proceedings of the California Academy of Sciences, Fourth Series, 28:1–24.

YONGE, C. M. 1960. Further observations on *Hipponix antiquatus* with notes on North Pacific pulmonate limpet. Proceedings of the California Academy of Sciences, Fourth Series, 31:111–119.